Rock climbing affects cliff-plant communities by reducing species diversity and altering species coexistence patterns

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ABSTRACT

Cliffs are unique ecosystems with an outstanding but relatively unknown plant diversity, harboring rare, endemic and threatened species, but also common and dominant species. The rising popularity of climbing represents an increasing threat to cliff biota, potentially diminishing diversity and species associations, and affecting the community composition. We used a novel closely paired sampling design in climbing routes with different climbing intensities in El Potrero Chico (Nuevo León, Mexico), differentiating plant species and analyzing species associations and community composition in climbed and unclimbed plots. Diversity on the sampled cliffs was high, even greater than in other regional ecosystems. We found reduced abundance, cover, and diversity in climbed plots, irrespective of the climbing intensity. Dominant species were the most negatively affected by rock climbing in terms of abundance, and some locally rare species, comprising endemics and endangered species, were entirely absent from climbed plots. Co-occurrence analysis showed that the number of associations between pairs of dominant and common species were greatly reduced in climbed plots, and that positive associations between locally rare species existed in unclimbed plots but not in climbed plots, which may contribute to the disappearance of endemic and threatened species. Finally, NDMS analysis revealed that the community composition significantly changed due to climbing. Our results indicates that conservation science should convince stakeholders of the need for a holistic conservation of cliff ecosystems and not only focus on emblematic or rare species, since the plant community dynamics and preservation depends on the coexistence and interactions between different plant species.

Keywords: Cliff plant community composition; Dominant and rare species; Human disturbance; Spatial associations; Species co-occurrence and interactions; Sport ecology.

INTRODUCTION

Cliffs are extreme ecosystems that harbor unique plant species diversity. Due to the heterogeneous cliff micro-topography and the accompanying variation in abiotic conditions, diverse plant species can colonize cliff crevices, despite the cliffs' harsh abiotic conditions for plant development (García-Callejas et al. 2021). Cliffs can include endemic and highly specialized species, comprising threatened species, which often are the focus of conservation purposes in these environments (deCastro-Arrazola et al. 2021). Whereas certain endemic, specialist and threatened species can be locally rare when their distribution range or local presence is restricted, some rock-specialists and generalist species can be frequently dominant on cliffs (Escudero 1996; March-Salas et al. 2018).

The spatial coexistence of functionally different species is one of the outstanding characteristics of cliff ecosystems (Farris 1995; Larson et al. 2000). Coexistence patterns and positive associations may arise from beneficial biotic interactions (e.g. shared fungal and bacterial communities, mutualistic interactions with floral visitors), from facilitation processes such as nutrients supply from plant litter decay or from differences in resource requirements (García-Callejas et al. 2021). Nevertheless, this coexistence, and underlying species associations, cannot be understood as a competitive factor in cliffs. Competition and negative associations lie in the colonization of the available micro-niches, since micro-spatial heterogeneity offers micro-niches with near plant-by-plant independence in space, and in nutrient and water resources (Cooper 1997; do Carmo et al. 2016). Rising climatic and anthropic pressures such as rock climbing could then hinder species coexistence and consequently affect the existing ecological associations in cliffs.

The great increase in climbing popularity and intensity is altering cliff plant communities and other cliff organisms including mosses, lichens, birds, and some invertebrates (Adams and Zaniewski 2012; Baur et al. 2017; Lorite et al. 2017; Schmera et al. 2018; Covy et al. 2019). Nevertheless, effects of rock climbing on species coexistence and associations and their consequences for the cliff community configuration remain unknown. Cliff plant communities are usually composed of dominant, common and rare species, each of them providing different functions due to their different relative densities, life-history and functional traits (Avolio et al. 2019; Gray et al. 2021). Thus, rock climbing may alter each of these ecologically different groups, their associations and ultimately, the cliff ecosystem itself. Dominant plants (considered as species that contribute greatly to the structure of an ecosystem due to their high relative density and abundance) can be diminished while locally rare species (i.e. low-abundant and locally uncommon species that might not be consistently rare throughout their geographical range; Murray and Lepschi 2004) could even disappear if the rock climbing pressure is high. The disturbance of beneficial associations among dominant and among locally rare species could impact the ecological stability of different ecosystems (Calatayud et al. 2020; Gray et al. 2021), but this question is unknown in cliff ecosystems. For instance, rock climbing could directly trigger an increase in the intra- and inter-species distance, alter the abundance of dominant species and eliminate both dominant and rare species (Larson et al. 2000). Rock climbing may also decrease the presence of mosses and lichens that help colonization of and nutrient acquisition by cliff plants, or obstruct plant accessibility to natural seed dispersers such as ants, birds or lizards. In turn, these effects of rock climbing indirectly affect plant community composition, its viability, and related biotic interactions (Farris 1995; Larson et al. 2000).

Conservation research mostly focuses on biodiversity, on the one hand, and rare species, on the other hand (Gaston 2010; Gray et al. 2021), whereas dominant and common species are frequently overlooked, even though they drive the community structure, facilitate other species colonization and make up a larger share of biomass in the ecosystem (Gaston

2010; Avolio et al. 2019). Differences in spatial dominance is notorious in cliff ecosystems, since cliff plants are not homogeneously distributed along the cliff face (Graham and Knight 2004). Thus, rock climbing can cause differential effects on species depending on their relative abundance and spatial distribution, as it has already been shown for generalist versus rock-specialist species (Müller et al. 2004; March-Salas et al. 2018). For instance, dominant species may be able to buffer the rock climbing impacts better than rare species, as shown under other environmental stressors and ecosystems (Sasaki and Lauenroth 2011; Qi et al. 2018), while some rare species could disappear. However, the number of individuals in dominant species could be greatly reduced if the climbing intensity increases, following observed trends of plant diversity as a whole (Clark and Hessl 2015; Lorite et al. 2017). As known in other ecosystems, a reduction of dominant or common species may affect the community configuration and their functionality (Avolio et al. 2019), and the loss of rare species could have dramatic consequences in terms of local or even overall biodiversity. Thus, species with dominant and common occurrence on cliffs would likewise deserve conservation efforts.

Furthermore, while most previous studies on the impact of rock climbing on cliff vascular plants have focused on the effects on plant cover and species richness, probably due to the relative low abundance of cliff plants, cliff species diversity (usually quantified by diversity indices) is little studied. Species diversity is more complex than species richness, since species diversity includes the abundance of each species to evaluate the number of species in a community. The quantification of plant diversity using diversity indices (e.g. Shannon-Wiener Index, *H'*; Simpson Index, *D*) can then be useful to better understand cliff species assemblies and their conservation value. These measures are assessed and well-known for most ecosystems and habitat types, but they have so far not been assessed in cliff ecosystems. Thus, studies should also focus on cliff diversity assessment in order to incorporate this as criterion for decision making in cliff management and for its biodiversity conservation.

This work presents the first study on cliff vascular plant communities in Latin America. It is conducted in El Potrero Chico, one of the most popular climbing destinations of the world. El Potrero Chico is a famous limestone valley and recreational park located within the “Sierra el Fraile y San Miguel” Natural Protected Area in Nuevo León, Mexico, holding a high conservation value. To test the rock climbing impact on its cliff plant abundance, cover, diversity, species associations and community composition, we use a closely paired design of climbed versus unclimbed plots by establishing a sampling quadrat along the cliff face (Boggess et al. 2021). In order to assess the role of increasing rock climbing pressures on cliff-plant species, we selected climbing routes with differing climbing intensities. The species were separated between locally rare, common and dominant species, in order to assess coexistence and associations in cliff ecosystems and whether rock climbing affects community composition.

Considering previous findings, we predict that (1) rock climbing negatively affects species cover, abundance, and diversity, and (2) that these negative effects of rock climbing increase with increasing climbing-use intensity. We explore for the first time how rock climbing affect dominant and rare species, and whether it may promote changes in species associations and community composition, as climbing routes can increase intra- and inter-species distance. For this we hypothesize that (3) the loss of individuals due to rock climbing is greater in dominant than in rare species but some locally rare species disappear in climbing areas; (4) that the number of positive species associations are lower in climbed versus unclimbed plots; and (5) that rock climbing alters cliff plant community composition. Testing these hypotheses is relevant for the development of effective conservation strategies for cliff ecosystems.

MATERIAL AND METHODS

Study site

El Potrero Chico (Nuevo León, Mexico) is located on the northern edge of the 'Sierra el Fraile y San Miguel' Natural Protected Area, which has an area of 23,506 ha between 800 and 2,360 m a.s.l. This area is part of the Sierra Madre Oriental mountain range, and it is composed of sedimentary rocks of marine origin dating back Mesozoic era, shale and limestone, the latter being the rocks that form the cliffs (INECC 2017), and the type of rock that holds more cliff vegetation and plant specialization processes (Farris 1995; Larson et al. 2000). El Potrero Chico has a semi-arid climate with hot summers (average monthly maximum temperatures over 35 °C between June and August) and moderate cold temperatures during winter (average monthly minimum temperatures between 7°C and 16°C). The highest precipitation is reached in September and October with averages ranging from 70 mm to 130 mm while the rest of the year monthly precipitation is below 50 mm.

El Potrero Chico is one of the world's prime climbing destinations with over 600 climbing routes within 24 climbing sectors. The first recorded climbing in El Potrero Chico was in 1960 but this sport experienced a great development in this area from late 1980s. Winter and early spring (between November and May) are the seasons with most climbers in this area due to the moderate temperatures cold and lowest precipitation, while the number of climbers is lower during the rest of the year due to the hot or rainy weather.

Sampling design

To examine differences between unclimbed and climbed areas, we designed a closely-adjacent case-control sampling design with a 3 m wide × 3 m high quadrat placed along the climbing route (Fig. S1). The quadrat was composed by a central Climbed (C) plot of 1m wide and 3 m high, two immediately adjacent plots of 0.5 m wide and 3 m high, which are not surveyed (*i.e.* no data was obtained from these plots), and two Unclimbed (U) plots of 0.5 m wide and 3 m high on the left and right side of the 3 m × 3 m quadrat that were used as controls, since they represent areas not reached by climbers (Fig. S1). The use of a closely adjacent paired design is essential to adequately test the impact of rock climbing on cliff vegetation (Boggess et al. 2021), since this precludes the possibility that variations in biotic or abiotic factors such as aspect, micro-topography and insolation could act as drivers of differences between climbed and unclimbed plots (Holzschuh 2016; Boggess et al. 2021). Closely-paired transects have the added benefit of avoiding an observer's interference in the undisturbed areas, since unclimbed transects can be surveyed from the same anchor with the help of directional gear placements (Boggess et al. 2021).

To define the position of the climbed plots (and thus, of the sampling quadrat), the bolts installed in the cliff-face were considered as the central point (i.e. 0.5 m to the right and 0.5 m to the left of the bolt), since the bolt represents with high precision the typical middle point that climbers use when ascending. However, to avoid interference with adjacent climbing routes, the selected routes for sampling were at least 5 m distant from the next climbing route. The unsurveyed plots are an adaptation from March-Salas et al. (2018) and guarantee separation between the unclimbed and climbed plots, since not all climbers follow exactly the same lane across a climbing route. This prevents any noise in the data acquisition from casual climber's ascent deviations, as unsurveyed areas cannot be considered completely undisturbed (Boggess et al. 2021). Moreover, in order to characterize the spatial distribution of plants within each plot, both climbed and unclimbed plots were divided in 0.5 m × 0.5 m subplots (i.e. 12 subplots in each climbed plot and 12 subplots in each unclimbed plot; *see* Fig. S2). Pictures were taken from each subplot (*see* below in 'Data collection').

To examine the maximum spatial distribution of cliff-face plants, we established the sampling quadrats at three heights along the climbing route, positioned at the Top, Middle and Bottom cliff-section (Fig. S1). In order to fit the three quadrats without any overlap, we selected climbing routes of between 15 m and 35 m height. The distance from the Middle to the Top and Bottom plot was roughly equidistant.

Data collection

Field surveys were conducted from November 2019 to December 2020. We sampled 12 climbing routes of El Potrero Chico (Table S1), adding up 36 climbed plots with a sampled area of 108 m^2 and 36 unclimbed plots with a sampled area of 108 m^2. The sampled routes were placed in contrasted aspects: North (n=5), South (3), East (1) and West (3). We noted the height of each climbing route as well as the climbing difficulty using the Yosemite Decimal System (YDS), grouped in three classes in our sampling sites: beginner (5.6–5.9), intermediate (510a–5.11d), advanced (5.12a–5.13d). To take into account the physical characteristics of the rock (i.e. micro-topography), we measured the slope of the center of each quadrat in the field, and the proportion of cracks (i.e. crevices) in each 0.5 m × 0.5 m subplot using *ImageJ*, and the estimated both measures at plot level. These measurements are crucial to eliminate potential bias when testing the climbing effect, since the establishment and survival of plants are more restricted under steeper and negative slopes, and under lower percentage of cracks (Larson et al. 2000; Holzschuh 2016).

To determine the climbing intensity of each route, we used the Climbing-Use Intensity (CUI) index (Clark and Hessl 2015), as a function of the walking time required to reach the cliff base and the popularity of the climbing route inferred by the number of stars (0–4) assigned in a reference and updated climbing guidebook of the area (Madden 2019). In order to use a standardized and categorized measure, we grouped the CUI values by quartiles (Clark and Hessl 2015), resulting in low (Q1), moderate (Q2), high (Q3) or very high (Q4) climbing intensity.

We noted all the plants present to calculate the species richness in the climbed and unclimbed plots of each route and quadrat, as well as the number of individuals per species (i.e. abundance). Unidentified species in the field were later identified through image determination by local botanical experts but 18 of the species could only be determined at the genus level. Species were further classified as endemic (species restricted to the Sierra Madre Oriental, Mexico), native (non-endemic but present in Mexico), and alien species (Velazco et al. 2011; Salinas-Rodriguez et al. 2017), and according to their rock association as rock-specialists (i.e. restricted to rocky habitats), species with non-strict but close association to rocky habitats (i.e. frequently inhabiting rocky environments but also found in other ecosystems) and generalist species. Shannon-Wiener (H') and Simpson (D) diversity indices were calculated per cliff as well as per climbed and unclimbed plot within each route using the *diversity* function from the *vegan R* package (Oksanen et al. 2020). Based on the pictures taken, plant cover was determined by the area (i.e. plant orthogonal projection) using *ImageJ* (in cm^2) and then calculated as the percentage of a plant's cover relative to the climbed or unclimbed plot. Additionally, the relative cover (CR_i), the relative abundance (AR_i) and the relative frequency (FR_i) of each species in the sampled plots were calculated (Alanís et al. 2020). Moreover, we classified species into dominant (DO), common (CO) and locally rare (RA) by using the Importance Value Index (IVI) of species (see below) together with the species distribution range and local presence (Curtis and McIntosh 1951; Velazco et al. 2011). IVI was calculated using the *importance value* function from the *Biodiversity R* package (Kindt and Coe 2005). IVI considers the sum of the relative frequency (number of plots where a species is observed divided by the total number of surveyed plots), the relative abundance (in terms of number of individuals of a species, also referred to as relative density) and the relative spatial dominance (in terms of percentage of rock area cover by a given species) of species. Thus, this determines the ecological value in terms of abundance and biomass and thus the dominance of the species in the plant's community (Curtis and McIntosh 1951). Species with the 15% highest IVI were considered as dominant species, species with the 15% lowest IVI were considered as locally rare species, and species with in-between IVI values were considered as common species (Table S2).

Data analysis

We conducted all statistical analysis with *R version 4.0.3* (R Development Core Team 2020). We used Linear Mixed-effects Models (LMMs) implemented in the *lme4* package and the *lmer* function (Bates et al. 2015) to test the effect of rock climbing (here in advance referred as climbing) on plant abundance, cover, and species richness, and whether this effect differed among different climbing intensity levels. Plant abundance, cover, and species richness were included as response variable in three separate models. Cliff section (three levels: Bottom, Middle, Top), climbing difficulty (three levels: beginner, intermediate, advanced), climbing effect (two levels: climbed vs. unclimbed), climbing intensity (four levels: low, moderate, high, very high) and the two-way interaction between climbing effect and climbing intensity were modelled as fixed factors. Climbing route nested in climbing sector was included as random factor, and the slope and the percentage of cracks as covariates. Additionally, in two separate models, we used LMMs including climbing effect as fixed factor and route nested in sector as random factor to test whether Shannon-Wiener and Simpson diversity indices calculated per study site (i.e. route) differed between climbed and unclimbed plots.

Furthermore, to detect patterns of co-occurrence among species in the sampled cliffs and whether this co-occurrence varies among the species-dominance level (i.e. rare, common, dominant species), we used the *cooccur* function from the *cooccur R* package (Griffith et al. 2016). This species co-occurrence analysis was conducted considering species occuring in the same route, same cliff section and same climbing effect, as interaction would occur at this spatial level. In this way, the presence/absence co-occurrence matrix of all species (Fig. S3) and the co-occurrence within climbed and within each unclimbed plots were analyzed and mapped separated by positive, negative (both considered as non-random associations) or random associations. Random associations are those that do not deviate from their expected co-occurrences by more than 0.1 considering the number of plots generated (Griffith et al. 2016). Only co-occurring species are shown in the matrix, so the analysis represents an approach of the number of species co-occurring, and thus coexisting and potentially interacting in each condition (i.e. by climbing effect and route section). Posteriorly, the number of co-occurrences between pairs of groups of species dominance level was also calculated. Moreover, we also used LMMs to test whether abundance and cover of the three dominance groups were differently affected by climbing. These models included the group of species dominance level (three levels: rare, common, dominant), climbing effect and their two-way interaction as fixed factors, and route nested in sector as random factor.

Finally, we tested for changes in community composition between sites due to climbing. To this aim, we first used permutational multivariate analysis of variance using distance matrices with the *adonis* function from the *vegan R* package (Oksanen et al. 2020) in order to assess the extent that factors influence the species composition while controlling permutations by routes (i.e. sites). Second, we implemented non-metric multidimensional scaling (NMDS) analysis to visualize and thus interpret the species configuration according to climbing, and among and within routes for testing for variation in species composition among and within communities. Here, we used the *MetaMDS* function of the *vegan R* package (Oksanen et al. 2020) that calculates Bray-Curtis distances for the community-by-site matrix.

In all LMMs, we tested the assumptions of normality and homogeneity of variance of the residuals using the Shapiro-Wilk test and the Bartlett test, respectively, and also checking it visually. If the residuals were not normally distributed, we transformed the response variable. In the case of heteroscedasticity, we applied a weighted least square regression (Strutz 2016) by including weights (1/variance) into the model, using the extract model *weights* command. Whenever there were significant main effects containing more than two levels or significant interactions, we applied post-hoc contrasts using the *lsmeans* package (Lenth 2016) with the Tukey’s test.

RESULTS

A total of 578 individuals from 63 species were recorded, corresponding to 52 genera and 30 families (*see* Table S2). Although the total surveyed climbed and unclimbed area was the same, we found 170 individuals of 37 species in climbed plots and 408 individuals of 52 species in unclimbed plots. The most frequent species (i.e. number of plots where the species is present) were *Agave lechuguilla* Torr. (n=21 plots), *Chrysactinia pinnata* S. Wats. (19), *Stenaria nigricans* (Lam.) Terrel. (17), *Cheilanthes standleyi* (Maxon) Mickel (15), and *Linum lewisii* Pursh (15). The least frequent species were *Echeveria elegans* Rose. (1), *Echinocereus enneacanthus* Engelm. (1), *Pinguicula gracilis* L. (1) and *Sedum palmeri* S. Watson. (1), among others (Table S2). The most abundant species (i.e. number of individuals per species) were *Chrysactinia pinnata* (n=51 individuals), *Cheilanthes standleyi* (49), *Agave lechuguilla* (46), *Stenaria nigricans* (41) and *Euphorbia prostrata* Aiton (25) (Table S2).

Four of the species found are listed in the IUCN Red List of Threatened Species: *Echeveria elegans* is listed as Endangered (EN) and was only found in unclimbed plots (Solís et al. 2011). *Agave bracteosa* S. Wats. Ex. Engelm., *Brahea dulcis* (Kunth) Mart. and *Dasylirion berlandieri* S. Watson are listed as Least Concern (LC). *Echeveria elegans* and *B. dulcis* are endemics considered as rock-specialist and rock-associated species, respectively, while *A. bracteosa* and *D. berlandieri* are both endemic and generalist species.

Climbing effect on cliff-species abundance, cover, and diversity

Plant abundance, cover and species richness were significantly lower in climbed plots than in unclimbed plots ($\chi_1^2 \geq 14.89$; $p < 0.001$; *see* Table 1). Plant cover was affected by a significant two-way interaction between climbing effect and climbing intensity while this interaction was neither significant for species richness nor for abundance (Table 1). Plant cover was lower in climbed plots in all climbing-intensity levels but the greatest differences between climbed and unclimbed plots were found in low (post-hoc test: $t = 4.397$; $p = 0.001$) or very high (post-hoc test: $t = 4.265$; $p = 0.002$) climbing intensity (Fig. 1). A significant effect of climbing intensity was found in species richness and a marginal effect was found in abundance (Table 1). Species richness and abundance were greater in high-intensity areas but post-hoc tests did not reveal significant differences between pairs of intensity levels ($t \leq 2.446$; $p \geq 0.095$). Species richness ($r = 0.84$), abundance ($r = 0.85$) and plant cover ($r = 0.68$) were significantly and positively affected by the percentage of cracks, and the abundance was significantly and negatively affected by cliff slope (Table 1). Moreover, neither climbing difficulties nor cliff sections had significant effects on plant richness, abundance and cover (Table 1). Additionally, climbing difficulty and its interaction with climbing effect were not significant in any of the variables ($\chi_2^2 \leq 3.299$; $p \geq 0.192$).

The overall mean Shannon-Wiener (H') and Simpson (D) diversity indices were 3.54 and 0.96, respectively. Shannon-Wiener diversity in climbed plots (overall $H'_C = 3.09$) was lower than that in unclimbed plots ($H'_U = 3.58$), and the mean Shannon-Wiener diversity index among sites was significantly lower in climbed plots than in unclimbed plots ($\chi_1^2 = 23.51$; $p < 0.001$; Fig. 2). Simpson diversity was lower ($D_U = 0.96$; $D_C = 0.93$) but not significantly different in climbed plots compared to unclimbed plots ($\chi_1^2 = 0.93$; $p = 0.334$).

Climbing effect on cliff-species associations and community composition

The species co-occurrence analysis revealed 18 non-random and 648 random associations in climbed plots (Fig. 3A), and 78 non-random and 1575 random associations between species in unclimbed plots (Fig. 3B). All 18 non-random associations in climbed plots were positive (Fig. 3), while 75 positive and 3 negative non-random associations existed in unclimbed plots. In unclimbed plots, negative associations were found between *Cheilanthes standleyi* (Dominant) and *Polygala sp.* (Dominant), and in *Chrysactinia pinnata* (Dominant) with *Tradescantia sp.* (Common) and *Bouvardia ternifolia* (Common). The taxa with the highest number of positive associations in climbed plots were *Helenium sp.* and *Croton fruticulosus*, both common species with four co-occurrences each. The taxa with the highest number of positive associations in unclimbed plots were *Notholaena sp.* (Common; N=10 positive associations), *Stenaria nigricans* (Dominant; 8), *Neoplinglea sp.* (Common; 8), and *Carlowrightia texana* (Common; 6). The analysis also showed that in unclimbed plots, four significant and positive associations existed between pairs of rare species (i.e. *V. coahuilensis – S. suffrutescens*; *Gochnatia sp. – C. cortesianus*; *P. oleracea – O. engelmannii*; *Linum sp. – N. intergrifolia*) but there were no relationships between pairs of rare species in climbed plots (Fig. 3). Moreover, in both, climbed and unclimbed plots, rare species were positively associated with common species but not with dominant species (Fig. 3).

The total number of co-occurrences detected between each possible pairs of species groups according to the dominance type (e.g. Dominant-Dominant, Dominant-Common, Dominant-Rare, etc.) was always lower in climbed compared to unclimbed plots (Fig 4; *see* raw data in Table S3). In addition, the number of individuals in dominant, common and rare species was lower in climbed plots compared to unclimbed plots (Fig. S4). However, while mean abundance in dominant or common species per route was significantly lower in climbed plots than in unclimbed plots (Dominant: t = 4.419; p = 0.001; common: t = 4.078; p = 0.003), mean abundance in rare species was lower but not significantly so in climbed plots than in unclimbed plots, probably due to the relatively low number of individuals in rare species (Fig. S4).

Moreover, we tested for variation in species composition inter- and intra-routes (i.e. changes among and within communities) by implementing NMDS among and within routes, respectively. Species composition significantly varied between routes ($F_{11,21}$ = 2.546; p = 0.001) but not within routes (i.e. no differences in species composition existed among bottom, middle and top sections within the routes; $F_{2,34}$ = 0.762; p = 0.776). Finally, NMDS analysis with 2,047 permutations showed that the composition of species significantly differed between climbed and unclimbed plots when controlled by site and section ($F_{1,21}$ = 1.116; p = 0.007; Fig. 5), so species composition differed due to climbing.

DISCUSSION

Our study in El Potrero Chico (Mexico) found a decrease in species diversity as well as a reduced number and type of associations between pairs of species caused by rock climbing, which led to a strongly altered cliff-plant community. Positive species associations that were significant in unclimbed plots disappeared in climbed plots, highlighting that climbing causes a lower number of positive associations between pairs of dominant species and the absence of beneficial coexistence between pairs of locally rare species. Losing rare species and their interactions due to climbing could trigger a local decline of endemic and threatened species. In our study, this was the case with *Echeveria elegans* (EN), which occurred in unclimbed plots but not in climbed plots. The negative effect of climbing observed for the association between pairs of different dominant species is also worrying, since dominant species drive community dynamics and facilitate interactions of other species even under harsh conditions (Qi et al. 2018), which is a distinctive feature of cliffs. The reduced species diversity and abundance observed in climbed versus unclimbed plots also goes together with decreased species coexistence. In this sense, our results strongly support that climbing and not intra-population variability drove cliff community composition.

Climbing impact on the presence and diversity of species

In line with our hypothesis, climbing negatively impacted abundance, plant cover, species richness, and species diversity in the cliff populations sampled in El Potrero Chico. Negative effects of climbing in plant abundance, cover and species richness were already documented in previous studies (e.g. Camp and Knight 1998; Lorite et al. 2017; March-Salas et al. 2018; Schmera et al. 2018). However, this is the first time that responses of plant species diversity to climbing in a cliff ecosystem were estimated, revealing relatively high diversity compared to other nearby regional ecosystems and negative effects from climbing. The Shannon-

Wiener diversity in the studied cliffs (*H*' = 3.54) was comparable and even higher than that of other ecosystems of Nuevo León (Mexico) such as temperate forest (*H*' = 0.72-1.74), thorny or submontane scrubland (*H*' = 1.94-3.02) and medium sub-evergreen forests (*H*' = 3.15), but lower compared to medium sub-deciduous forests (*H*' = 4.29-5.80) (Alanís et al. 2020). However, climbed routes had a 14% lower diversity at the study site, and probably climbing could sometimes even cause an indirect negative effect on unclimbed areas by hindering inter- and intra-species interactions and cliff-colonization, reducing the total cliff plant species diversity. Maintaining relatively high diversity is essential for cliffs communities functioning and ecosystem preservation.

Contrary to our expectations, climbing had a negative impact irrespective of the climbing intensity. Negative impacts were found at each level of climbing use intensity and this impact did not increase with increasing intensity. Indeed, the strongest difference in plants cover between climbed and unclimbed plots was found at low and at high climbing intensity, reflecting the absence of any linear patterns with climbing intensity. This result matches relatively well with observations in climbing areas of Jura Mountains (Switzerland) of Schmera et al. (2018) but contradicts previous studies showing that climbing effects strongly depend on climbing intensity (Clark and Hessl 2015; Lorite et al. 2017). The absence of linear patterns with climbing intensity may be explained because the greatest impact of climbing likely occurs during the opening of a new route, since route equippers (i.e. persons in charge to establish the route in the cliff by incorporating metal anchors) frequently remove plants and mosses to facilitate the climbers' ascent. Also, first ascents could be more impactful for cliff plant communities. Thus, the impact would not increase significantly with increasing frequency of climbers, as indicated by Schweizer et al. (2021). They studied how lichen cover in a boulder changes during simulated increasing climbing frequency. They found that the effect of climbing is strongest during the first 50 ascents and that subsequent ascents did not cause any further significant damage, meaning that the climbing impact on lichen cover stabilized over time. Thus, an assessment of plant community over time starting from undisturbed primal cliffs, followed by the opening of new routes, and the increase of climbing activity is required to confirm this unsolved question.

Changes in cliff species associations and community

Rare species are particularly threatened by various anthropogenic threats (Vitousek et al. 1997), but literature on the impact of climbing on rare species is scarce. Eleven of the locally rare species were found in unclimbed plots, but only three locally rare species occurred in climbed plots. Five of these rare species present in unclimbed plots are specialized on cliff habitats and all the rare species present in climbed plots were generalists. The loss of rare species in an ecosystem is worrisome, since rare species make up a large share of the diversity of ecological assemblages and promote positive interactions (Calatayud et al. 2020). Therefore, the disappearance of locally rare species would not only decrease diversity in cliff ecosystems, but also alter beneficial biotic interactions (*see* below). Remarkably, *E. elegans*, listed as Endangered species (EN), was only found in unclimbed plots, suggesting that climbing may burden rare and threatened species. The negative climbing effects found on species diversity and on the presence of endemic, rare and threatened species evidence that diversity indices together with endemic status and conservation values are all essential for framing adequate local conservation strategies.

As might be expected, the greatest total loss of individuals due to climbing occurred in dominant species. Dominant and other common species have at times been undervalued in conservation actions (Gaston 2010), but the loss of individuals of dominant species could significantly impact community structure (Avolio et al. 2019) and affect species establishment (Gilbert et al. 2009) and ecosystem structure or visualization, proportional to their abundance and biomass in the system (Avolio et al. 2019; Gray et al. 2021). In cliff ecosystems, dominance associates with abundance, frequency and cover, and depends on the available ecological micro-niche. The IVI values in our study system ranged from 0.17 to 9.33, being relatively low compared to some ecosystems such as woodlands (e.g. Didita et al. 2010) but otherwise higher than in other plant communities such as agroforests and thorny shrublands (e.g. Asigbaase et al. 2019). Due to the patchy structure and heterogeneity of the cliff face (Kuntz and Larson 2006; do Carmo et al. 2016), direct competition is almost absent in cliffs. Cliffs are usuall not totally covered by plants and therefore different cliff species are only seldomly sharing exactly the same abiotic resources (e.g. soil nutrients, water, light), restricting competition to the spatial occupation of available micro-niches (Kelly and Larson 1997; Larson et al. 2000). However, species with greater adaptive capacity and plasticity (e.g. having greater dispersal abilities in cliff environments, well-adapted root traits, drought tolerance strategy, greater plant cover) would be more abundant and dominant on the rock face (Larson et al. 2000), which may help communities to buffer the increasing environmental variability (e.g. March-Salas et al. 2021). The spatial organization of individuals and species in cliff ecosystems reflects important assemblage processes. In cliffs, dominant species could attract more pollinators, have reduced distance among individuals, lower rock erosion and provide more substrate to other cracks through litter decay, so positive interactions could appear between distinct groups of species. Thus, dominant species should be also considered when designing cliff protection measures, since they are essential for the maintenance of the ecosystem, especially under environmental or human disturbances such as climbing (Langenheder et al. 2012).

Our analysis shows for the first time significant species associations in cliff ecosystems (but *see* Cooper 1997), and these statistical species associations may reflect beneficial ecological interactions between species (Holt 2017). The total number of associations between pairs of species was 60% lower in climbed compared to unclimbed plots and positive associations were 73% lower in plots subjected to climbing. These declines may affect the dynamics of cliff populations. In addition, results of unclimbed plots show significant positive associations among various rare species. Paired rare-rare species associations existed in unclimbed plots but disappeared in climbed plots, suggesting the strong fragility of this type of biological interaction to anthropogenic perturbations (Vitousek et al. 1997; Schatz et al. 2014). The existence of positive associations between pairs of rare species in unclimbed plots is remarkable, considering their low abundance.

Our analysis also indicated that dominant and other common species would have positive effects and may facilitate rarer species, as has been found in other ecosystems (Smith and Knapp 2003). In unclimbed plots, the highest number of co-occurrences existed between different dominant species, and positive associations were found between them. In climbed plots, only two positive associations between dominant species existed and positive associations between common species accounted to 45% of all positive co-occurrences. Co-dominance is a common phenomenon that occurs when two or more species are similarly dominant in a biotic community, and studies show that dominant associations may indirectly favor establishment and even population growth of rare species, since it may control the presence of other common species (Avolio et al. 2019), in line with our results in unclimbed plots. Studies also suggest that co-dominance is an important driver of community structure and functioning, promoting long-term community stability (Smith and Knapp 2003; Crutsinger et al. 2008; Gray et al. 2021). Overall, climbing reduced all types of potential species associations. However, three negative associations were found in unclimbed plots, all involving dominant species, suggesting competition for the colonization of available micro-niches, or simply dispersal limits or an effect of general occurrence in the investigated area. Cliffs offer resource-poor patches and show spatial niche partitioning, so co-existence of different species capable of adapting to diverse conditions and positive co-dominance are essential for successful habitat colonization and functioning in these ecosystems (Gray et al. 2021).

Changes in species diversity and species associations resulted in a significant change in plant community composition due to climbing. The community composition varied among routes but not within the same route, suggesting that climbing would affect different community assemblages and that climbing, rather than any other potential drivers, is the main factor affecting the composition within cliff plant communities. If the change in species composition persists, it may jeopardize the structure and stability of cliff communities. This is especially true if this change triggers the loss of unique species or relevant biotic interactions, as was found in this study, and under the current climate change context (Ives and Carpenter 2007).

Conservation of cliff plant communities in climbing areas

Generally, the consequences of losing rare species at community or even ecosystem level are poorly understood (Jain et al. 2014), even though rare species are the focus of conservation efforts (Gaston 2010). Our findings point out that a loss of rare species will lead to a decrease in the number and type of species associations, potentially affecting ecological assemblages and rare species persistence (Calatayud et al. 2020). However, our insights highlight that conservation in cliff ecosystems should also focus on dominant species and their interactions, as well as on species diversity, since they can act as a buffer against disturbances and environmental variability, promote positive associations with common and rare species, and ultimately maintain cliff plant community functioning (Langenheder et al. 2012). In this sense, conservation science should convince stakeholders of the need for a holistic conservation of cliff ecosystem and not only focus on emblematic or rare species. In addition, the shift in the community assemblage and the absence of patterns regarding climbing intensity suggest that conservation efforts should focus on determining priority areas for conservation rather than merely trying to limit the impact on climbing routes itself. This includes controlling the opening of new routes, and identifying areas with low conservation value for continuing rock climbing activity in certain “safe areas” based on research studies. Conservation criteria should then not only concentrate on specific taxa or species groups, but rather focus on all rare, common and dominant species and their interactions, as well as on the maintenance of species diversity for long-term conservation success of cliff ecosystems.

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STATEMENTS & DECLARATIONS

Author's Contributions

FMA and MMS designed the study and MMS and JL designed the field-sampling methodology. FMA conducted the field surveys and gathered the data with the help of AS, while EEC helped to identify the cliff-plant species. MMS and JHA analyzed the data. MMS wrote the first draft of the manuscript with all coauthors contributing to revisions.

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Data Availability

Data will be made available in a public repository upon acceptance for publication.

Figure captions

Figure 1: Effect of climbing on mean species richness (**A**), abundance (**B**) and plant cover (in %) (**C**) per climbing-intensity level. Bar-plots (Means ± SE) of the two-way interaction between climbing effect and climbing intensity are shown for each variable (*see* Table 1).

Figure 2. Effect of climbing on the Shannon-Wiener diversity index at the study sites. **A.** Mean Shannon-Wiener diversity index ± SE by sampled sites is shown in the bar plot for climbed and unclimbed plots. **B.** Shannon-Wiener diversity present in each site (i.e. sampled route 'r'). Grey and white colors represent climbed and unclimbed plots, respectively.

Figure 3. Presence/absence co-occurrence matrix of species growing in climbed (**A**) and unclimbed (**B**) plots. Pairwise co-occurrences were restricted to species found in the same site and cliff-section and separated between those co-occurring in each climbed (A) or unclimbed (B) plot. Positive associations are colored in blue, negative associations in yellow and significant random associations in grey. The species pair combinations without any observed or expected co-occurrence according to the analysis were removed by default, and therefore are not shown in the matrix. The level of dominance is highlighted in bold for each of the species. 'DO' refers to dominant species, 'CO' to common species and 'RA' to locally rare species.

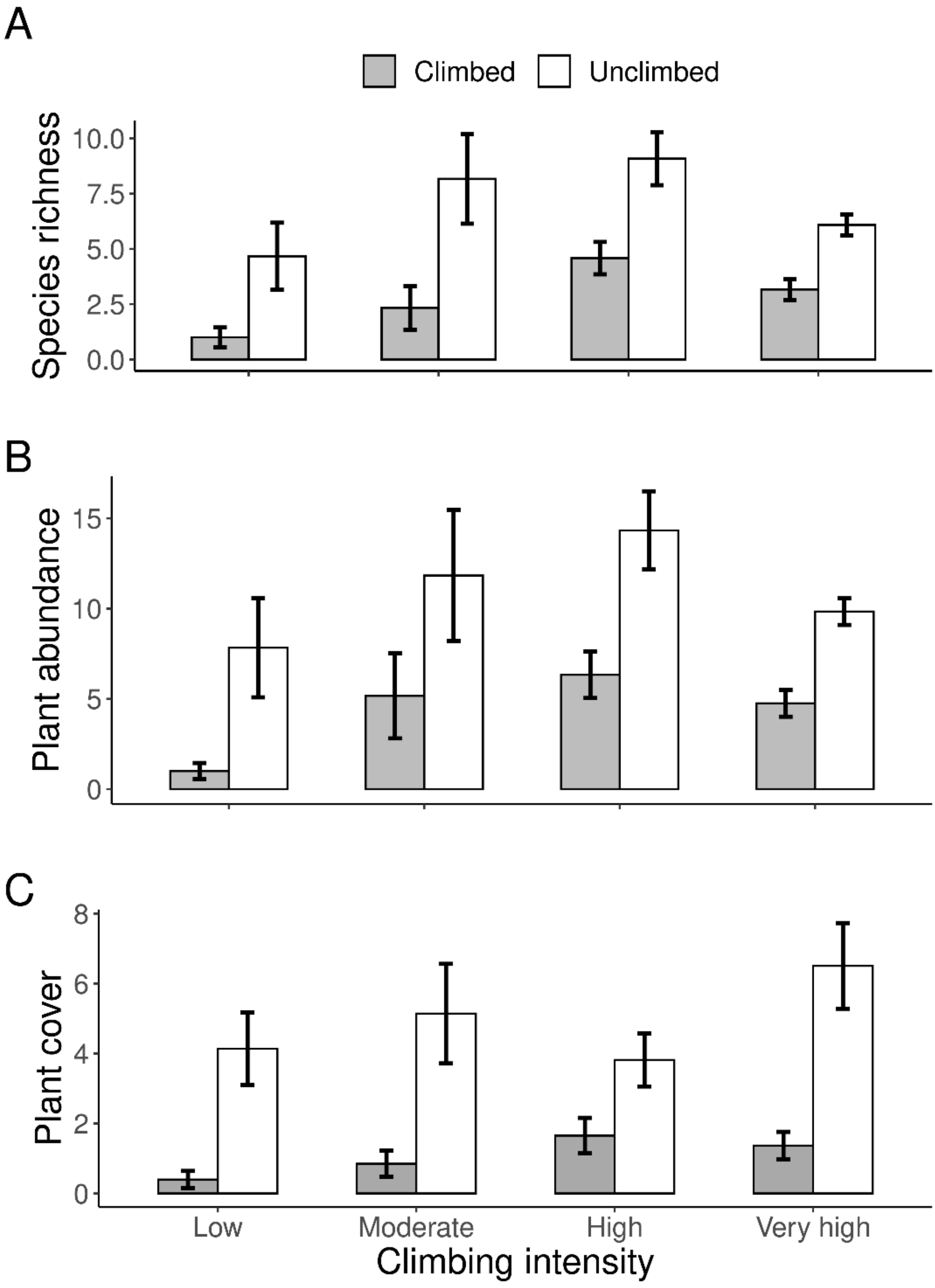
Figure 4. Number of co-occurrences (log transformed) between paired dominance groups of species calculated for unclimbed plots (in white) and for climbed plots (in grey) growing in the same site and cliff section. 'DO' refers to dominant species, 'CO' to common species and 'RA' to locally rare species. Raw data are shown in Table S3.

Figure 5. Biplot showing variation in species composition between climbed and unclimbed plots. Predicted values of the species two-dimensional spatial configuration with regard to NMDS1 and NMDS2 axes are shown. Polygons show differential species composition

between climbed and unclimbed plots according to the NMDS analysis. Each point represents a single species, and symbols and colors divide species into dominant, common, and rare.

Figures

Figure 1



736 **Figure 2**

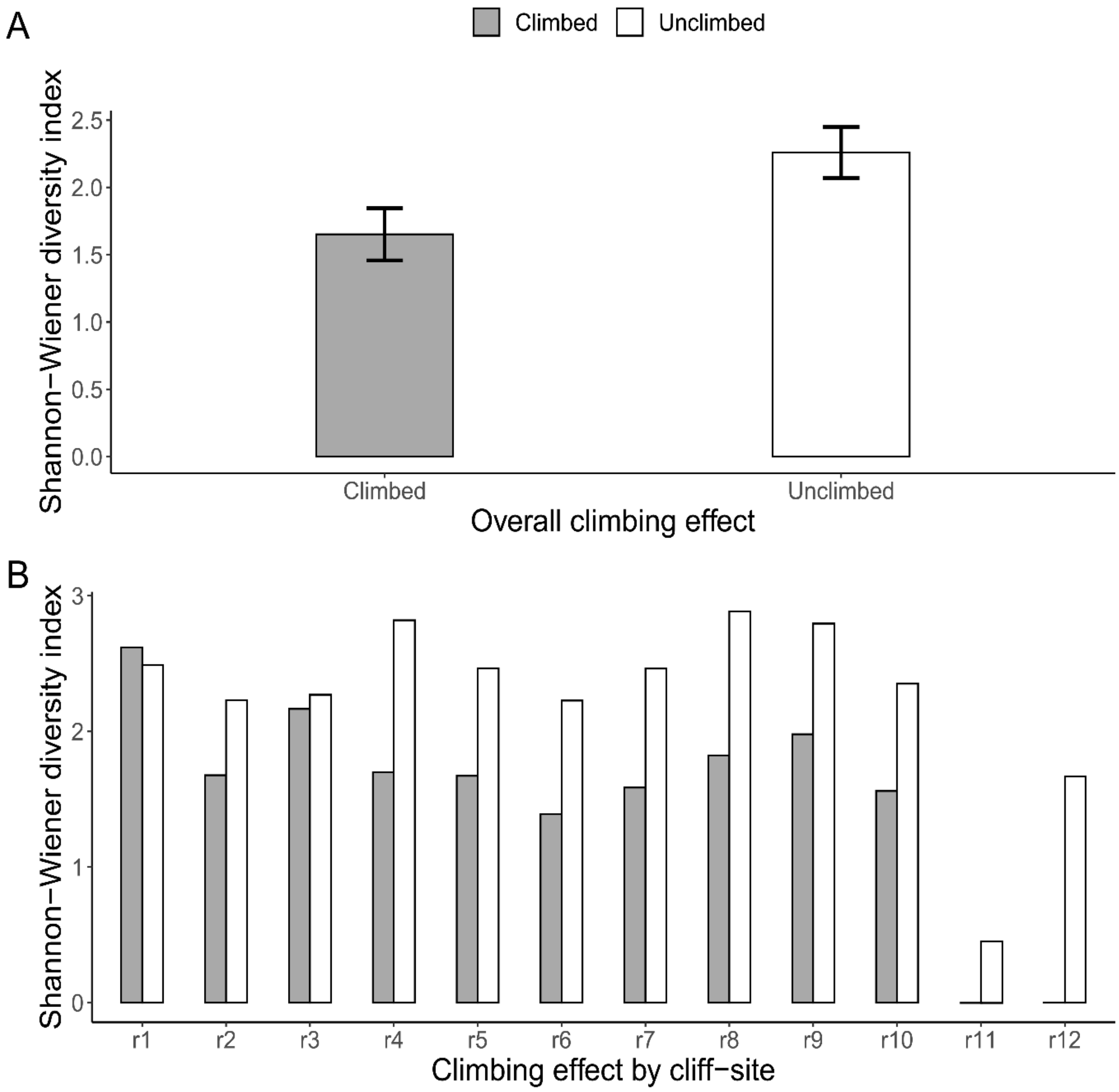


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Figure 3

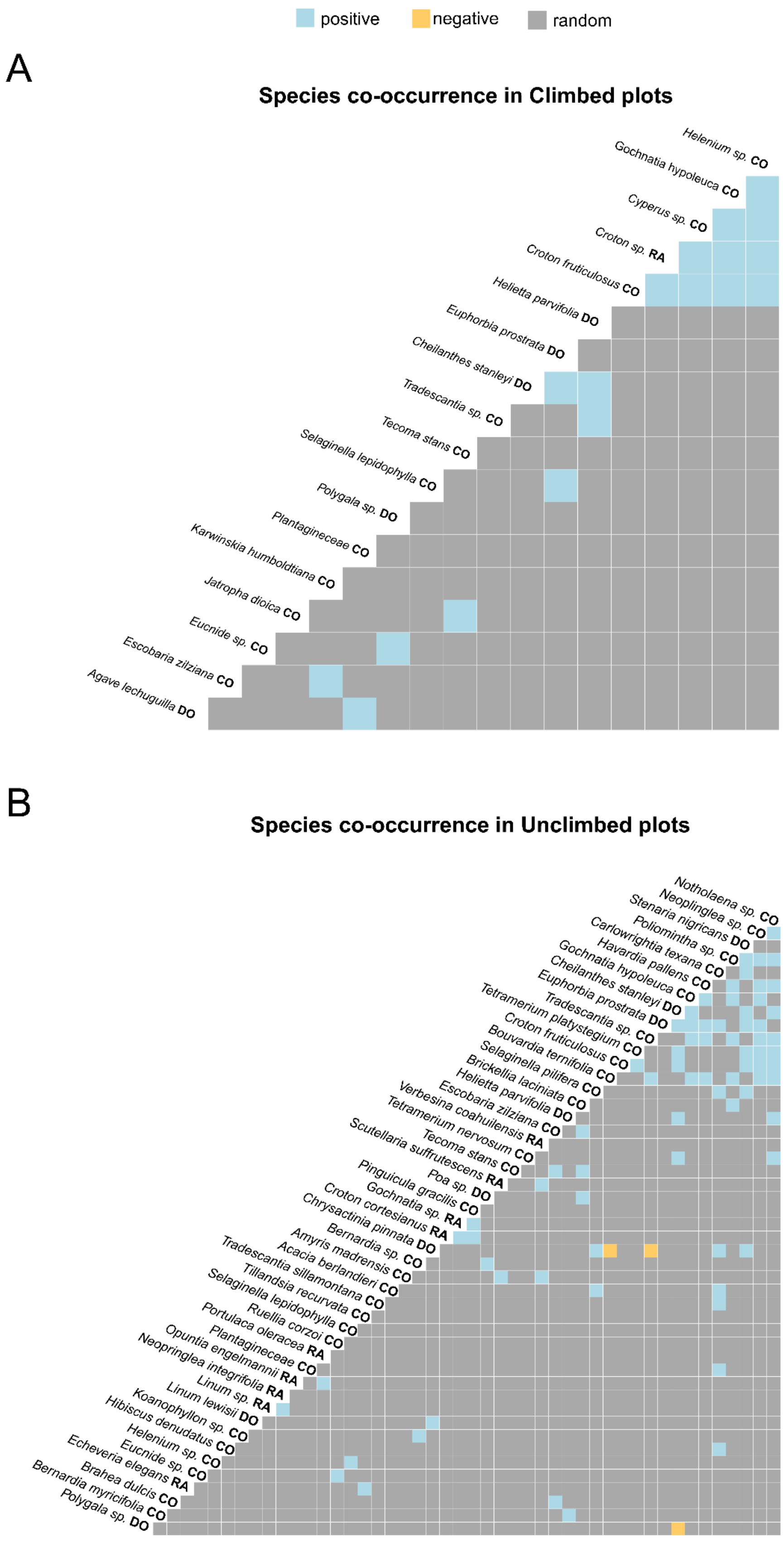
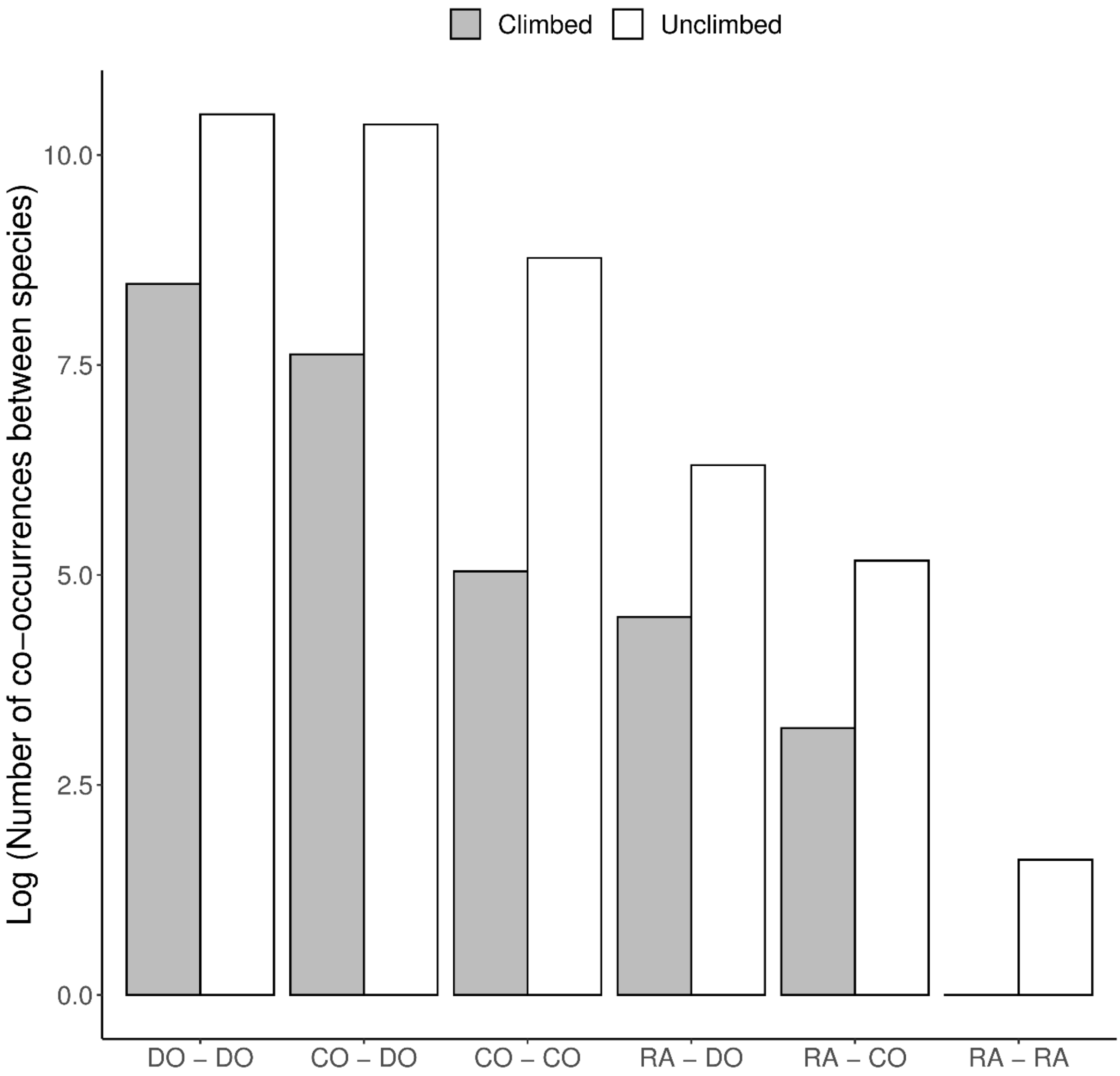
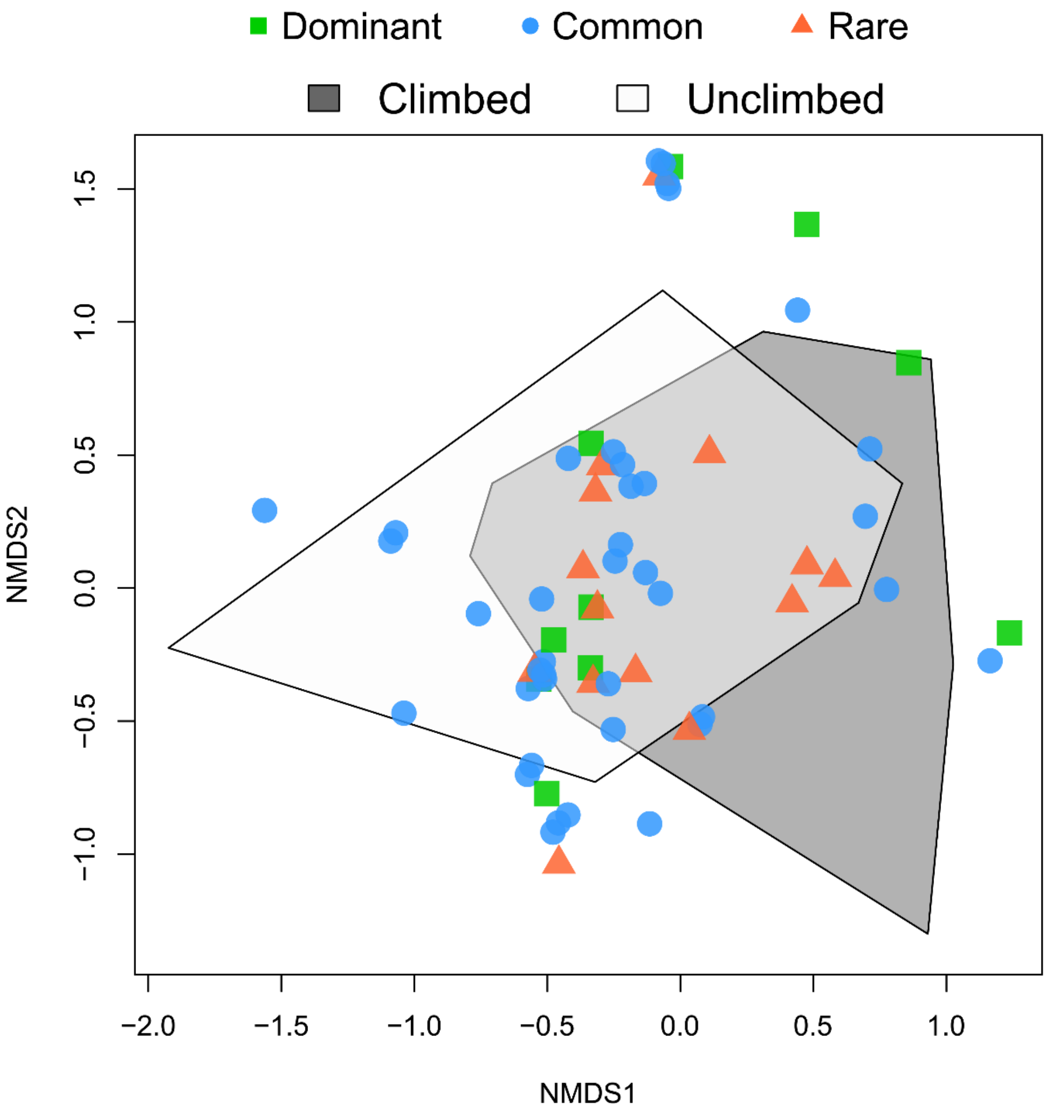

positive
negative
random
A
Species co-occurrence in Climbed plots
Helenium sp. CO
Gochnatia hypoleuca CO
Cyperus sp. CO
Croton sp. RA
Croton fruticulosus CO
Helietta parvifolia DO
Euphorbia prostrata DO
Cheilanthes stanleyi DO
Tradescantia sp. CO
Tecoma stans CO
Selaginella lepidophylla CO
Polygala sp. DO
Plantagineceae CO
Karwinskia humboldtiana CO
Jatropha dioica CO
Eucnide sp. CO
Escobaria zilziana CO
Agave lechuguilla DO
B
Species co-occurrence in Unclimbed plots
Notholaena sp. CO
Neoplinglea sp. CO
Stenaria nigricans DO
Poliomintha sp. CO
Carlowrightia texana CO
Havardia pallens CO
Gochnatia hypoleuca CO
Cheilanthes stanleyi DO
Euphorbia prostrata DO
Tradescantia sp. CO
Tetramerium platystegium CO
Croton fruticulosus CO
Bouvardia ternifolia CO
Selaginella pilifera CO
Brickellia laciniata CO
Helietta parvifolia DO
Escobaria zilziana CO
Verbesina coahuilensis RA
Tetramerium nervosum CO
Tecoma stans CO
Scutellaria suffrutescens RA
Poa sp. DO
Pinguicula gracilis CO
Gochnatia sp. RA
Croton cortesianus RA
Chrysactinia pinnata DO
Bernardia sp. CO
Amyris madrensis CO
Acacia berlandieri CO
Tradescantia sillamontana CO
Tillandsia recurvata CO
Selaginella lepidophylla CO
Ruellia corzoi CO
Portulaca oleracea RA
Plantagineceae CO
Opuntia engelmannii RA
Neopringlea integrifolia RA
Linum sp. RA
Linum lewisii DO
Koanophyllon sp. CO
Hibiscus denudatus CO
Helenium sp. CO
Eucnide sp. CO
Echeveria elegans RA
Brahea dulcis CO
Bernardia myricifolia CO
Polygala sp. DO

Figure 4



Climbed
Unclimbed
Log (Number of co-occurrences between species)
10.0
7.5
5.0
2.5
0.0
DO – DO
CO – DO
CO – CO
RA – DO
RA – CO
RA – RA

Figure 5


Dominant
Common
Rare
Climbed
Unclimbed
NMDS2
NMDS1
1.5
1.0
0.5
0.0
−0.5
−1.0
−2.0
−1.5
−1.0
−0.5
0.0
0.5
1.0

Tables

Table 1. Climbing effect on species richness, abundance and plant cover. To show whether the climbing effect varies among climbing intensity levels, we included climbing effect (Climbed vs. Unclimbed), climbing intensity and their two-way interaction in the Linear Mixed-effect Models (LMMs). The percentage of cracks (Perc. cracks) and cliff slope were included in the LMMs as these abiotic factors may affect the climbing impact. Cliff section (Bottom, Middle, Top) was included to assess whether the presence of plants or their coverage vary with cliff height. Transformations applied to the response variable are indicated after the variable name. Significance is shown as * $0.05 > p$; ** $0.01 > p \geq 0.001$; *** $p < 0.001$, and · refrects marginal effects ($0.1 > p \geq 0.05$).

Response variable	Parameter	Chi-Square	df	p-value	
Species richness					
	Perc. Cracks	58.834	1	<0.001	***
	Slope	0.201	1	0.654	
	Cliff-section	0.052	2	0.975	
	Climbing difficulty	1.497	2	0.473	
	Climbing effect	15.324	1	<0.001	***
	Climbing intensity	19.299	3	<0.001	***
	Climbing effect × intensity	1.508	3	0.680	
Abundance ^ 0.6					
	Perc. Cracks	55.547	1	<0.001	***
	Slope	4.423	1	0.035	*
	Cliff-section	1.266	2	0.531	
	Climbing difficulty	3.177	2	0.204	
	Climbing effect	25.358	1	<0.001	***
	Climbing intensity	7.201	3	0.066	·
	Climbing effect × intensity	1.561	3	0.668	
Plant cover ^ 0.3					
	Perc. Cracks	20.320	1	<0.001	***
	Slope	2.324	1	0.127	
	Cliff-section	0.237	2	0.888	
	Climbing difficulty	0.007	2	0.997	
	Climbing effect	28.911	1	<0.001	***
	Climbing intensity	1.715	3	0.634	
	Climbing effect × intensity	11.513	3	0.009	**

SUPPLEMENTARY INFORMATION

Table S1. Sampled cliffs and their geographic coordinates.

Climbed cliffs	Coordinates
1. The Virgin Canyon	25°56'58.51"N - 100°28'41.38"W
2. Buzz Rock	25°57'15.71"N - 100°29'01.66"W
3. Wonder Wall	25°57'00.65"N - 100°28'36.80"W
4. Cañón de los Lobos	25°57'02.00"N - 100°28'32.02"W
5. Land of the free	25°57'06.76"N - 100°28'53.57"W
6. Mota Wall	25°56'50.51"N - 100°28'33.20"W
7. La Ola	25°56'54.21"N - 100°28'29.60"W
8. Blubber Wall	25°56'43.04"N - 100°27'51.73"W
9. Fitness Cave	25°56'32.61"N - 100°27'52.03"W
10. Outrage Wall	25°56'52.56"N - 100°28'38.38"W

Table S2. List of plant species and families found in the study sites. Species are classified according to their distribution (native, endemic or alien). The frequency (i.e. number of plots where the species is present) and abundance (i.e. number of individuals) of each species found in the study sites are shown. Finally, the type of rock association separating into generalists (G), rock-specialists (S) and species with non-strict but close association to rocky habitats (A) is shown.

Plant specie	**Family**	**Distribution**	**Frequency (F)**	**Abundance (A)**	**IVI**	**Rock-association**
Acacia berlandieri	Fabaceae	Native	2	2	0.75	G
Agave bracteosa	Asparagaceae	Endemic	9	19	4.66	G
Agave lechuguilla	Asparagaceae	Native	23	46	9.33	G
Amyris madrensis	Rutaceae	Native	1	1	0.37	G
Bernardia myricifolia	Euphorbiaceae	Native	2	2	0.42	G
Bernardia sp.	Euphorbiaceae	-	4	19	2.13	G
Bouvardia ternifolia	Rubiaceae	Native	6	7	1.48	G
Brahea dulcis	Arecaceae	Endemic	4	4	2.00	A
Brickellia laciniata	Asteraceae	Native	5	5	1.15	G
Carlowrightia texana	Acanthaceae	Native	8	15	2.53	G
Cheilanthes standleyi	Pteridaceae	Native	15	49	5.30	S
Chrysactinia pinnata	Asteraceae	Endemic	19	51	7.33	G
Croton cortesianus	Euphorbiaceae	Native	1	1	0.20	G
Croton fruticulosus	Euphorbiaceae	Native	7	7	1.86	G
Croton sp.	Euphorbiaceae	Native	1	1	0.20	G
Cyperus sp.	Cyperaceae	-	2	2	0.64	G
Dasylirion berlandieri	Asparagaceae	Endemic	2	2	0.84	G
Echeveria elegans	Crassulaceae	Endemic	1	1	0.22	S
Echinocereus enneacanthus	Cactaceae	Native	1	1	0.27	A
Escobaria zilziana	Cactaceae	Endemic	6	6	1.14	A
Eucnide sp.	Loasaceae	Native	2	4	0.59	G
Euphorbia prostrata	Euphorbiaceae	Native	10	25	3.13	G
Gochnatia hypoleuca	Asteraceae	Native	5	9	1.99	G
Gochnatia sp.	Asteraceae	Native	1	1	0.17	G
Havardia pallens	Fabaceae	Native	4	5	1.71	G
Hechtia podantha	Bromeliaceae	Endemic	3	3	0.68	A
Helenium sp.	Asteraceae	Native	2	11	1.03	G
Helietta parvifolia	Rutaceae	Native	9	18	3.13	G
Hibiscus denudatus	Malvaceae	Native	3	5	0.80	A
Jatropha dioica	Euphorbiaceae	Native	1	1	0.76	G

Karwinskia humboldtiana	Rhamnaceae	Endemic	1	1	0.54	G
Koanophyllon sp.	Asteraceae	-	3	3	0.61	G
Linum lewisii	Linaceae	Native	15	20	3.45	G
Linum sp.	Linaceae	Native	1	1	0.24	G
Lobelia sp.	Campanulaceae	-	3	8	0.93	A
Mammillaria heyderi	Cactaceae	Native	5	10	1.36	A
Mirabilis sp.	Nyctaginaceae	-	1	1	0.27	A
Neoplinglea sp.	Salicaceae	-	6	6	1.43	G
Neopringlea integrifolia	Salicaceae	Native	1	1	0.28	G
Notholaena sp.	Pteridaceae	Native	8	11	1.81	S
Opuntia engelmannii	Cactaceae	Native	1	1	0.22	G
Pinguicula gracilis	Lentibulariaceae	Endemic	1	3	0.31	S
Plantaginacea	Plantaginaceae	-	6	12	1.69	G
Poa sp.	Poaceae	-	13	22	3.76	G
Poliomintha sp.	Lamiaceae	Native	8	10	2.07	G
Polygala sp.	Polygalaceae	Native	9	16	3.62	S
Portulaca oleracea	Portulacaceae	Alien	1	1	0.18	G
Ruellia corzoi	Acanthaceae	Endemic	1	2	0.32	G
Salvia sp.	Lamiaceae	Native	1	1	0.18	G
Scutellaria suffrutescens	Lamiaceae	Native	1	1	0.22	G
Sedum palmeri	Crassulaceae	Endemic	1	1	0.18	A
Selaginella lepidophylla	Selaginellaceae	Native	3	11	1.03	S
Selaginella pilifera	Selaginellaceae	Native	4	12	1.22	S
Stenaria nigricans	Rubiaceae	Native	17	41	6.13	G
Tecoma stans	Bignoniaceae	Native	4	6	2.40	G
Tetramerium nervosum	Acanthaceae	Native	3	4	0.81	G
Tetramerium platystegium	Acanthaceae	Native	8	11	2.13	A
Tetramerium sp.	Acanthaceae	Native	2	2	0.36	A
Tillandsia recurvata	Bromeliaceae	Native	1	4	0.40	A
Tradescantia crassifolia	Commelinaceae	Native	7	19	2.54	G
Tradescantia sillamontana	Commelinaceae	Endemic	2	2	0.37	A
Tradescantia sp.	Commelinaceae	Native	5	10	1.89	G
Verbesina coahuilensis	Asteraceae	Endemic	1	1	0.27	S
			303	**578**		

Table S3. Number of co-occurrences between paired dominance groups calculated for all sites and cliff sections, and for unclimbed and climbed plots. ‘DO’ refers to dominant species, ‘CO’ to common species and ‘RA’ to rare species.

Paired groups	Treatment	Number of occurrences
DO - DO	Overall	60,680
CO - DO	Overall	54,420
CO – CO	Overall	9,374
RA – DO	Overall	875
RA – CO	Overall	297
RA – RA	Overall	4
DO – DO	Unclimbed	35,753
CO – DO	Unclimbed	31,692
CO - CO	Unclimbed	6,473
RA - DO	Unclimbed	548
RA – CO	Unclimbed	175
RA – RA	Unclimbed	4
DO – DO	Climbed	4,748
CO – DO	Climbed	2,049
CO – CO	Climbed	154
RA – DO	Climbed	89
RA – CO	Climbed	23
RA – RA	Climbed	0

Figure S1: The experimental sampling design consists of a quadrat of 3 m high × 3 m wide which is positioned in the bottom, middle and top sections of the cliff face along each sampled route. Each quadrat is divided into five plots: a central climbed plot of 3 m high × 1 m wide (C), two immediately adjacent plots of 3 m high × 0.5 m wide each (in dark grey) which was not surveyed, and other two adjacent unclimbed plots f 3 m high × 0.5 m wide on each side (U) that represent the areas not frequented by climbers (adapted from March-Salas et al. (2018)).

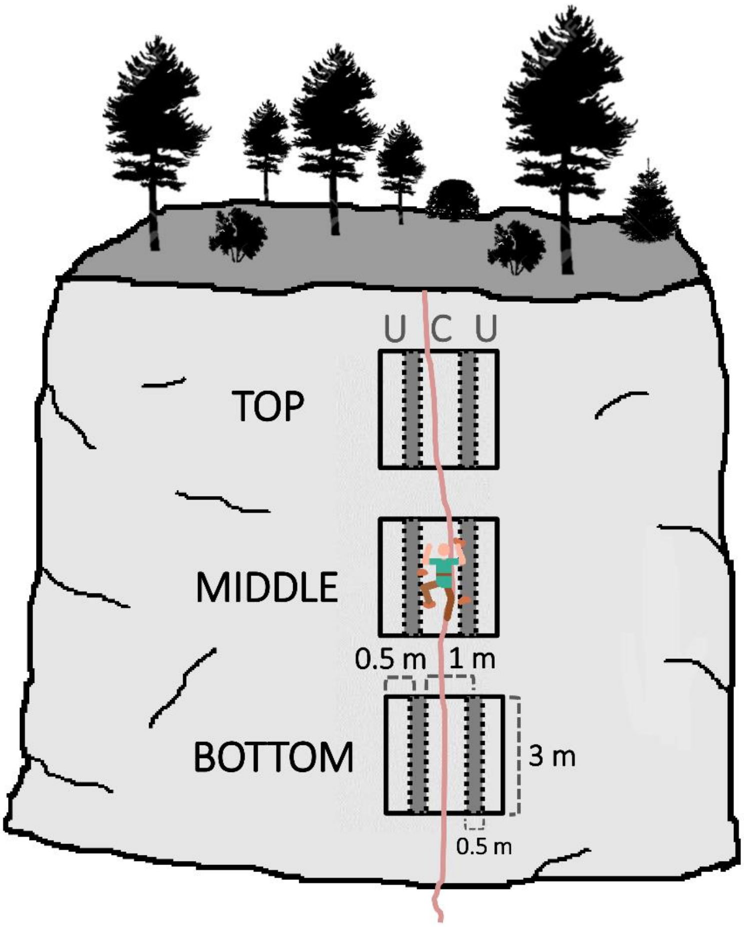


Figure S2. Overview of the sampling-quadrat design. The 3 m × 3 m sampling quadrat was divided in 0.5 m × 0.5 m subplots. Thus, both unclimbed and climbed plots were divided into 12 subplots. 'L', 'R' and 'C' letters represents left, right and central areas, respectively. The grey part represents the unsurveyed area of the quadrat.

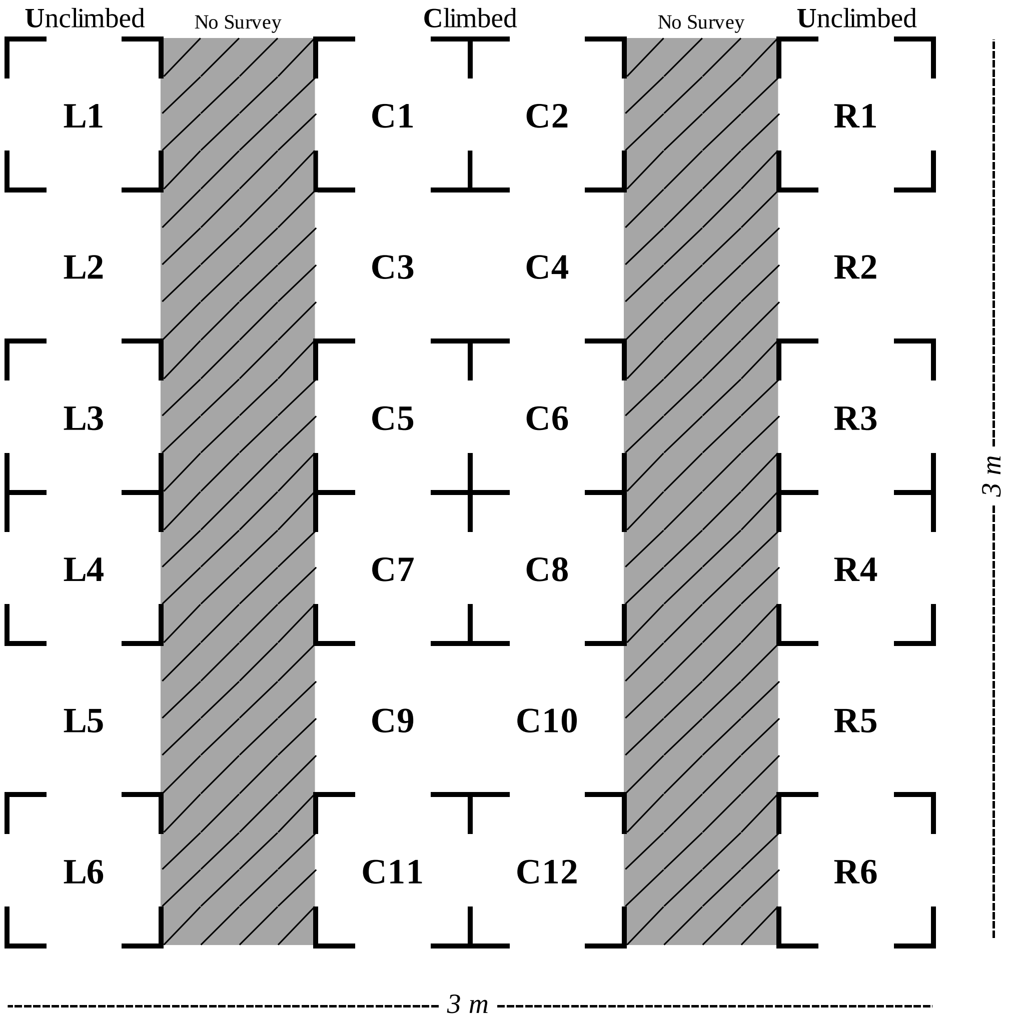


Figure S3. Co-occurrence matrix of presence/absence of the overall species growing in the same site and cliff section. Positive associations are colored in blue, negative associations in yellow and random associations in grey. The level of species dominance is highlighted in bold for each of the species. 'DO' refers to dominant species, 'CO' to common species and 'RA' to rare species.

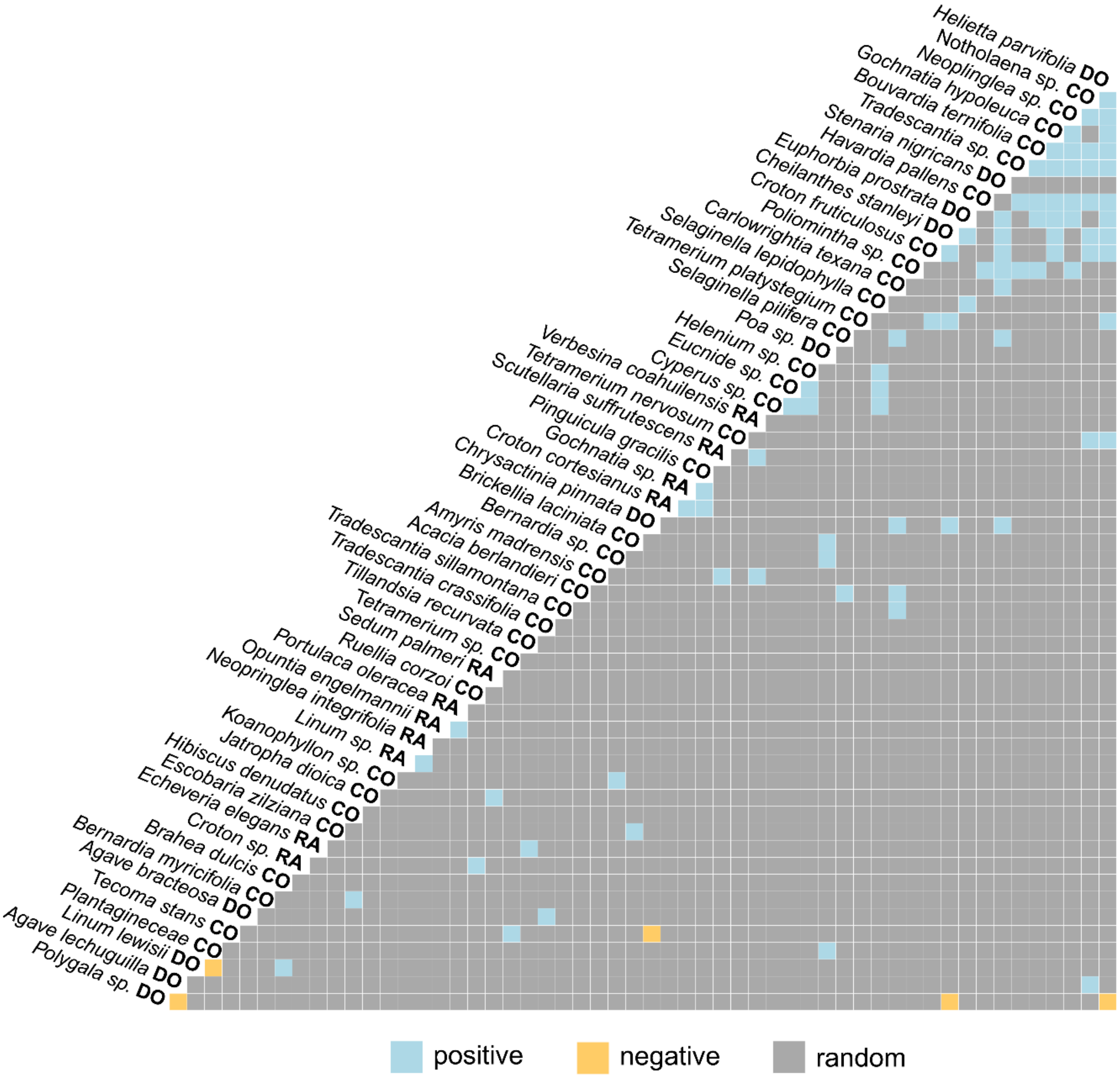


Figure S4. Mean plant abundance among routes by species dominance level in climbed and in unclimbed plots. The bars show the differences in mean number of individuals ± SE in dominant, common and rare species by climbed and unclimbed plots.